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Quaternary Vegetation History

ABSTRACT

The geological record reveals that Sierra Nevada ecosystems are a transitory part of a dynamic and evolving landscape. The effects of climatic change and disturbance events, however, can persist in time, and many ecological processes have long time spans. Therefore, the complete understanding of the current state of an ecosystem and its potential behavior, its adaptability and resilience, may require knowing its history over many hundreds to thousands of years. The Quaternary period is a geologic name for the past 2.4 million years, during which global climate cooled and at least six successive major glacial cycles covered the Sierra Nevada with ice caps and mountain glaciers, filled lake basins in the adjacent deserts, and lowered the elevation limits of plant species. These ice ages were interspersed with shorter warm intervals when arid habitats expanded into northerly latitudes and tree lines gained elevation. Species responded individualistically to these changes, sometimes assembling into communities with no known modern analog. During the peak of the last glaciation, 18,000 to 20,000 years ago, alpine vegetation, dominated by sagebrush and herbs, grew in a dry glacial climate above 1,500 m (4,900 ft) in the Sierra Nevada where there is now montane forest. At the same time a juniper woodland occupied the lower mountain slopes and desert basins of the eastern Sierra Nevada and an expanded bristlecone and limber pine forest covered the crest of the White-Inyo Mountains. As the glaciers waned after 14,000 years ago, dense conifer forests of a species mix unlike any modern assemblage were established in wetter climatic conditions at intermediate west-slope elevations. With continual warming after around 10,000 years ago, a dry, open conifer forest with a montane shrub understory and an increased number of oaks was growing throughout the range. Greater proportions of charcoal indicate an increase in fire frequency. Higher temperatures are also documented by an upslope extension of tree lines and the expansion of xeric desert species on the east side. Effective precipitation increased after about 6,000 years ago, as indicated by an increase of subalpine conifer populations and the closure of montane forests. Subsequent to 4,000 to 3,000 years ago, the apparent downslope retreat of whitebark pine, mountain hemlock, red and white fir, and incense cedar suggests an intensification of cooler conditions and the formation of the modern Sierran forests. A brief warm-dry period between A.D. 900 and 1300 was followed by a 400-year phase with average conditions cooler and wetter than today and multiple advances of alpine glaciers. Both climatic episodes are recorded in the paleoecological record.

INTRODUCTION

Time is the issue. Why is the history of Sierra Nevada vegetation over many thousands of years important to the Sierra Nevada Ecosystem Project (SNEP)? Ecologists know that the assessment of the condition and trend of an ecosystem requires measurements on the scale at which it operates (Scholes 1990). This is as true for temporal scales as it is for spatial scales. Ecosystems are dynamic and evolving. They have a history that can be hidden, because many ecosystem processes and changes occur at timescales greater than the timescale at which they are usually observed (Magnuson 1990; Scholes 1990). Serious errors can be made, for example, in the attempt to model the behavior of a plant community if there is a time lag in the response of that community to an external disturbance and if existing community structure is a result not of present conditions but of the persistence of a past effect.

Long time intervals cannot be practically studied with biological methods of observation and experiment. Historical records of climatic variables and evidence of past conditions provided by photographs and documents are too limited. Geological records of past environments, covering time periods of centuries to millennia, are becoming increasingly avail-

Sierra Nevada Ecosystem Project: Final report to Congress, vol. II, Assessments and scientific basis for management options. Davis: University of California, Centers for Water and Wildland Resources, 1996.

able. Although they have lower temporal, spatial, and biotic resolution than contemporary observations, they do reveal the response of vegetation to long-term variation in climate and disturbance regimes.

The reconstruction of Sierra Nevada vegetation through such proxy records as pollen and macrofossil (visible to the naked eye) stratigraphies and plant macrofossils from pack rat middens has the potential to define natural ranges of variability and trajectories for vegetation along a broad continuum of time frequencies. Paleoecological information can also help to identify thresholds, rates of change, successional pathways, and time lags; assess community stability and resilience to disturbance; specify the effective independent and dependent variables involved in change; and provide a baseline for the assessment of the relative influence of past, current, and future human activities.

The objectives of this paper are to (1) outline the climatic chronology of the Quaternary period as a context for the vegetation history of the Sierra Nevada; (2) briefly describe the methods used in the reconstruction of past vegetation; (3) summarize findings concerning vegetation dynamics and its relation to climate; (4) review and summarize the current literature on the Quaternary vegetation history of the Sierra Nevada study area; and (5) address possible management implications of our understanding of the vegetation history of the Sierra Nevada ecosystem.

QUATERNARY CHRONOLOGY

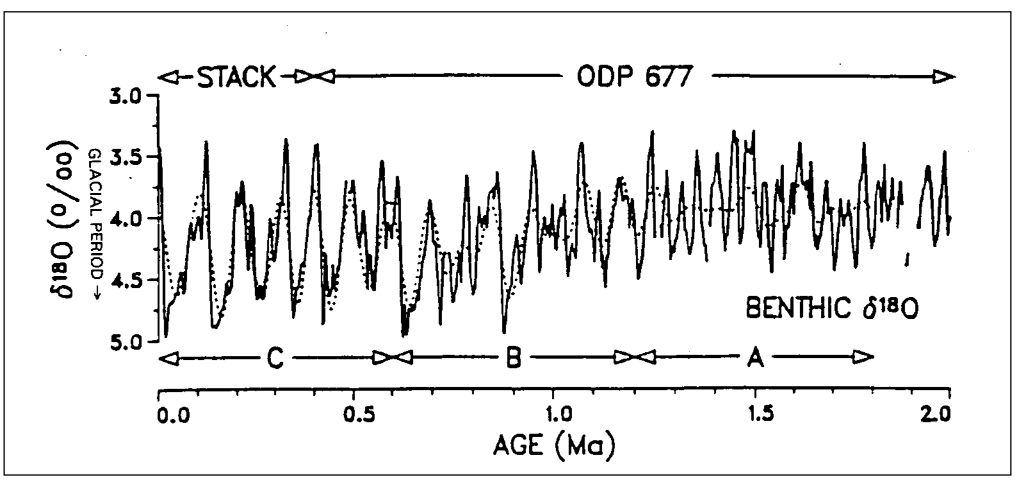
The Quaternary vegetation history of the Sierra Nevada can be more fully understood if it is placed in the context of the global climatic chronology because climate is a major driver of vegetation dynamics. Conventional time-stratigraphic nomenclature is used in this chapter (Coleman et al. 1987). When it is convenient, chronometric ages are abbreviated ka and Ma (thousand and million years, respectively, measured from the present). Thus, one thousand years ago is abbreviated 1.0 ka. Radiocarbon (^{14}C) ages are given as years before the present (yr B.P.), which is fixed at A.D. 1950: for example, 1200 yr B.P. Radiocarbon ages corrected for variation in the amount of ^{14}C produced in the atmosphere by calibration with the bristlecone pine tree-ring chronology is given as cal yr B.P. When calendar dates are precisely known from historical documents or tree-ring chronologies, they are given as B.C. or A.D.

The Quaternary period includes the Pleistocene and Holocene (or Recent) epochs. The Pleistocene was classically defined as a unique time when major glaciations occurred. This concept has somewhat lost its distinguishing characteristic with evidence of ice ages occurring throughout Earth's history since the early Precambrian over two billion years ago. Most recently, during the middle Miocene about 14 million years ago, the Antarctic ice sheet rapidly grew and mountain glaciers formed in the northern hemisphere (Flint 1971; Ghil 1991; Singh 1988). Nevertheless, the inception of the latest extensive continental glaciation is signaled by a rapid drop in levels of carbonate about 2.4 million years ago, documented in marine sediment cores from the North Atlantic Ocean (Ruddiman et al. 1990; Shackleton et al. 1984). This drop indicates the influx of ice-rafted particles from the ice sheets bordering the Atlantic that diluted the carbonates precipitating from seawater.

Chemical and microfossil analyses of marine sediments in deep ocean cores have provided continuous, high-resolution records of glacial-interglacial cycles throughout the Quaternary (Imbrie et al. 1992) (figure 4.1). Temporal variation in the distribution of foraminifera (a microscopic marine organism) assemblages reflect past temperature and salinity of ocean waters, and oxygen-isotope ratios ($\delta^{18}O$) extracted from the carbonate tests of these organisms provide estimates of temperatures and continental ice volume. The results of this research have been the resolution of what previously had been thought to be four glacial periods into at least eleven during

FIGURE 4.1

A benthic $\delta^{18}O$ record from the Atlantic Ocean for the past two million years (from Imbrie et al. 1992).



the last 900,000 years. At least six of these are recognized in the Sierra Nevada.

One of the dominant research questions in Quaternary science has been the causes of the Pleistocene ice ages. The initiation of continental glaciation has been attributed to changes in the coupled atmospheric and oceanic circulation system, which responded to such tectonic events as the closure of the isthmus of Panama and the uplift of the Sierra Nevada, Himalaya-Tibetan plateau, and other ranges (Ruddiman and Kutzbach 1989). The pattern of glacial oscillations is widely assumed to be driven by the seasonal and latitudinal distribution of incident solar radiation according to periodic variations in the earth-sun geometry (termed the Milankovitch theory, after the Yugoslav astronomer Milutin Milankovitch, who calculated and linked the orbital periodicities to climate changes [Berger 1991]). There are three major components: a 100,000-year cycle of the eccentricity (circular to elliptic) of the earth's orbit, a 41,000-year cycle of the earth's obliquity with respect to the ecliptic plane (variation in the tilt of the polar axis between 21.8° and 24.4°), and a 23,000-year precession of the equinoxes (the wobble of the earth's axis) (figure 4.2). Climatic information derived from ocean sediments, from ice cores taken from the Greenland and Antarctic ice caps, and from cores taken from terrestrial sedimentary basins has exhibited patterns that reflect these periodicities and demonstrate their influence on phenomena that are responsive to climate change. The combined effect of these geometric relationships produced the strong 100,000-year glacial-interglacial rhythm beginning about 700,000 years ago. Prior to this time the 41,000-year frequency dominated, with apparently weaker glacial expansions. Within these cycles, glacial periods averaged about 90,000 years, and warm interglacial periods averaged 10,000–20,000 years. The present Holocene climate phase, which began approximately 10,000 years ago, is the latest interglacial. Although it may be either halfway through or nearing its conclusion, the predicted global warming resulting from the injection of anthropogenic "greenhouse gases" into the atmosphere may be modifying the ancient climatic pattern.

Global ice volume grows with low summer insolation and high winter insolation and vice versa. There are also "free" oscillations generated by internal system feedback mechanisms and a large chaotic component. The presence or absence and limits of land and sea ice, sea surface temperatures, land albedo, effective soil moisture, composition of the atmosphere, and circulation of the atmosphere and oceans are other variables that can act as external forcing functions or internal variations, depending on scale. In general, external controls cause the large-scale variations over time and space, and internal controls operate on smaller scales, inducing continuous short-term variation (Bartlein 1988).

During the last deglaciation, summer solar radiation increased and winter solar radiation decreased from near present levels at 18,000 years ago to a summer maximum and winter minimum at 9,000 years ago. According to the computerized atmospheric general circulation models (GCMs) (COHMAP Members 1988; Kutzbach and Guetter 1986), major trends in climatic components include a decrease in land ice and an increase in sea surface temperatures, carbon dioxide, atmospheric dust, and—particularly important for vegetation change—seasonal variation in insolation (figure 4.3). Maximum summer insolation at 9,000 years ago caused the sustained above-average warm period known as the "early Holocene xerothermic" or "mid-Holocene climatic optimum," depending on the region affected. A rise in global temperature affects atmospheric circulation and, consequently, the position, orientation, and steepness of temperature gradients and precipitation patterns on a regional scale. So, while the northwestern United States became dry, the monsoons expanded and delivered increased summer rainfall to the Southwest, with resulting changes in vegetation.

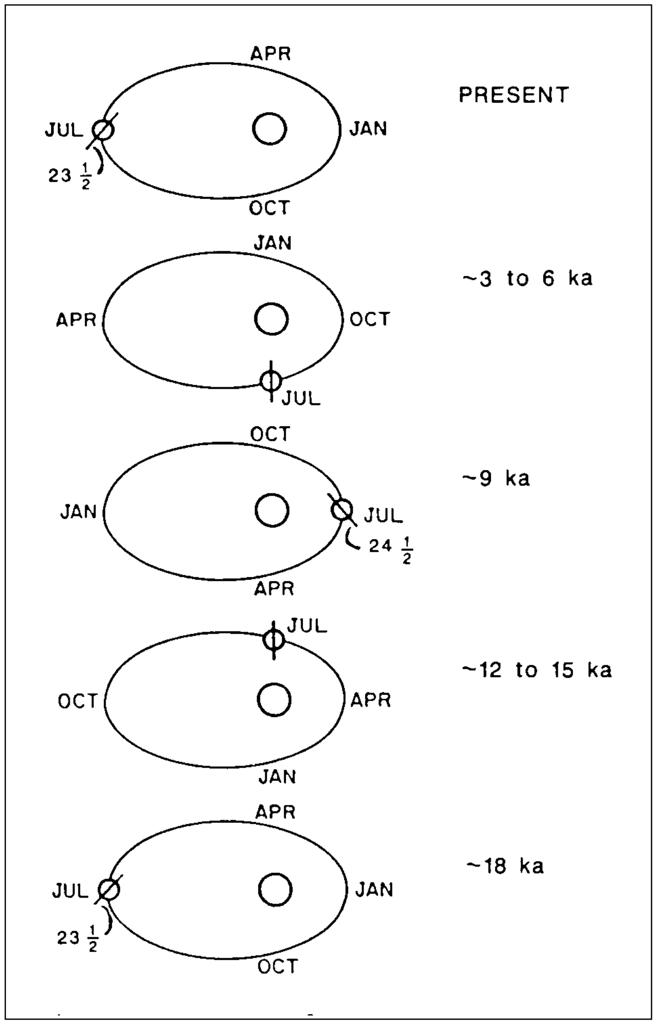


FIGURE 4.2

Earth-sun geometry at selected time intervals (from Wright et al. 1993).

At a smaller timescale another effect on the recent global

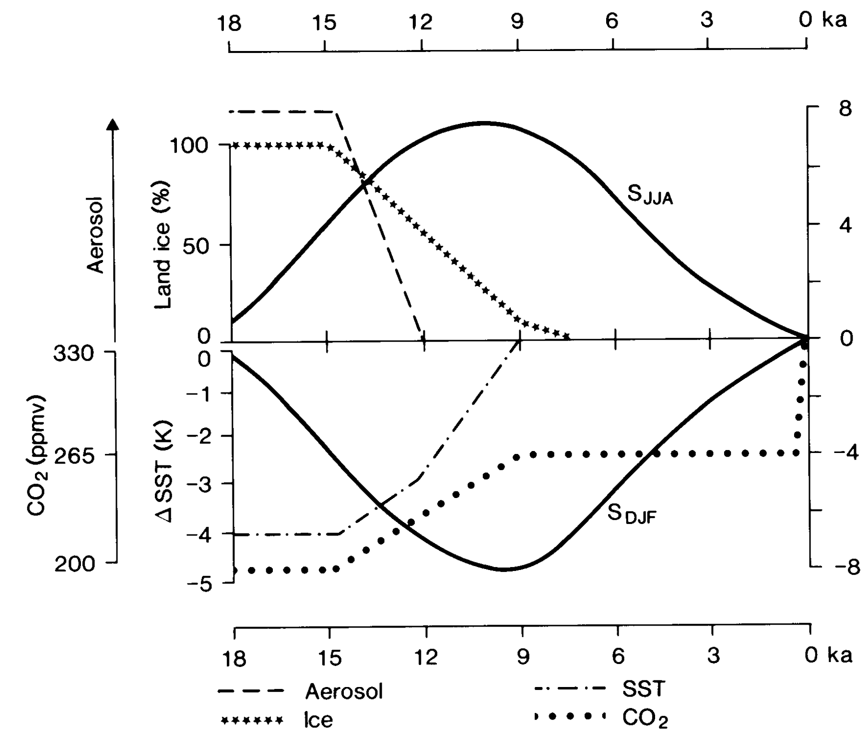


FIGURE 4.3

Boundary conditions for the COHMAP simulation with the Community Climate Model (from Wright et al. 1993).

climate system is the variation of solar irradiance. A correlation between the intensity of solar activity and global warming has recently been established by calibration with the radiocarbon (^{14}C) chronology (Damon and Sonett 1991). The history of solar activity through observation of sunspot cycles since the seventeenth century and recent systematic studies of solar irradiance are linked to the radiocarbon record. The increase in solar winds as the sun becomes more active blocks the cosmic rays that produce the radioactive isotope of carbon; thus, ^{14}C production is inversely related to irradiance. Therefore, a 9,000-year radiocarbon record, taken from carbon isotopes in long tree-ring records, can be used as a proxy for solar activity and, indirectly, a proxy for global temperature variations (Davis 1994). Times of minimum solar activity (high ^{14}C production) between A.D. 1400 and A.D. 1850 correspond to the Little Ice Age. The time of maximum irradiance between A.D. 1100 and A.D. 1300 approximates the Medieval Warm Period (Hughes and Diaz 1994; Stine 1990). Patterns of climate thus vary both periodically and irregularly at all spatial-temporal scales and must be taken into account when modeling vegetation change (figure 4.4).

The surface of the earth is like a palimpsest with traces of former landscapes becoming more obscured with the passage of time. Thus, more detail is known about the most recent climatic events. We view the last glacial period (generally termed the Wisconsinan) from the vantage point of a warm interglacial peak, which we consider normal. Since the previous interglacial, which peaked about 125,000 years ago, global cooling has been accompanied by brief, warmer excursions, producing an irregular sawtooth pattern when the temperature curve is plotted. During the glacial maximum global surface temperature averaged 4°C less than that of today, ice covered one-third of the land surface of the earth, sea level was about 121 m (397 ft) below the present sea level, and atmospheric circulation patterns were modified (COHMAP Members 1988; Kutzbach and Guetter 1986). Global climate was predominantly a winter-precipitation regime. The expanded land and sea ice strengthened the latitudinal temperature gradient, displacing westerlies southward and weakening the summer monsoon. Pacific frontal storms were tracked into California farther south than today, possibly throughout much of the year due to the contraction of the northern Pacific high-pressure cell. Lower summer temperatures and greater effective moisture led to the filling of large lake basins in the Great Basin and southeast California and the altitudinal and latitudinal displacement of many plant species compared to modern distributions; elevational ranges of species were depressed more than 1,000 m in the SNEP study area. Locally in the southern Sierra Nevada, the climate was cold and dry. This greater continental climate regime may be attributed to exposure of the California continental shelf due to lowered sea levels, which captured much of the precipitation arriving onshore (Barnosky et al. 1987).

VEGETATION-CLIMATE RELATIONSHIPS

As with climate, vegetation has changed within a hierarchy of time and space. At issue here is the relationship of processes between different scales, especially which processes become dominant at higher or lower levels. Consideration of the time and space scale at which observations of vegetation change are made is important in determining how closely vegetation has tracked climate change (Cole 1985; Davis 1986; Prentice et al. 1991; Webb 1986).

On a fine scale of less than a century and within a plant community domain of about one hectare (2.47 acres) (which is also at a human scale of observation), there is an apparent stability of process, structure, and species composition and abundance classes, in spite of constant turnover through loss and recruitment. A conventional pollen record may show longer periods (100 to 1,000 years) of regional vegetation stability relative to the local dynamic equilibrium of disturbance and succession (Bradshaw 1988). Usually, however, relatively gradual as well as abrupt changes in vegetation composition are described by the higher-order timescales of regional pollen diagrams. Equilibrium and successional trend models, concepts of habitat type, and potential vegetation in ecology have been based on short-term observations. Newer, alternative concepts of thresholds and multiple, nonlinear pathways among many possible states of species composition are more compatible with the insights of vegetation dynamics gained by longer-term observations through paleoecological methods (Tausch et al. 1993).

If climate, soil genesis, and allogenic disturbances could be held stable, biotic processes alone would be sufficient to produce change, most likely a modification of species abundances. With a combination of disturbance events and climate change, a regenerating plant community that was established under a different climate may produce an altered composition and structure as it responds to new climatic conditions (Patterson and Prentice 1985, 100). An extreme example of the effect is the ghost forest of Whitewing Mountain (3,050 m [10,000 ft]) on the Inyo National Forest. Several hectares of prostrate logs litter the crest of the now bare, pumice-covered ridge, which is located southeast of the town of June Lake in the eastern escarpment of the Sierra Nevada. Below tree line, an east-side red fir–mixed conifer forest grows on the slopes of the mountain and surrounding pumice flats. According to a radiocarbon (^{14}C) date of about 900 yr B.P. from a wood sample taken from one of the logs, the forest was growing during a warm period. The source of the pumice has been identified as the nearby Glass Creek volcanic vent, which erupted about 720 yr B.P. (Miller 1984). The forest was apparently blown down by the eruption and never regenerated, perhaps because the growing season was becoming too short as the climate cooled within the following

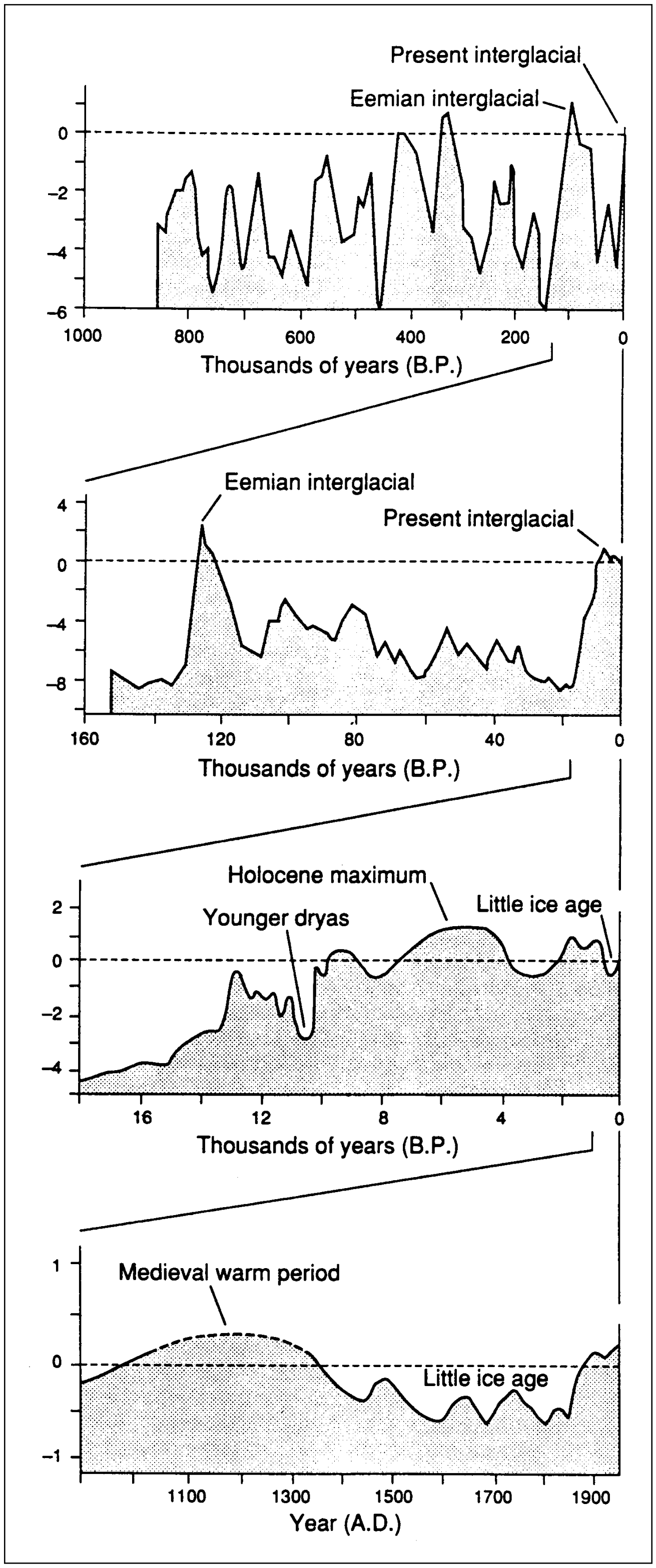


FIGURE 4.4

Global surface temperatures at four timescales (from Tausch et al. 1993; reprinted by permission of the Society for Range Management).

200 years (Graumlich 1993), preventing primary succession. At present only a few small individuals of whitebark pine are growing near the crest.

Disturbance events and variations in temperature and precipitation are by no means the only causes of vegetational change. Wide fluctuations in atmospheric carbon dioxide are being recognized as having had a major effect on ecosystems (Betancourt et al. 1993; Polley et al. 1993). For example, a recent study (Van De Water 1993) showed that a 40% increase in carbon dioxide at the last deglaciation was accompanied by a 17% decrease in stomatal density and a 14% increase in reconstructed water use efficiency in fossil limber pine. From these data it is hypothesized that the rise in atmospheric levels of carbon dioxide "influenced the ability of C3 plants to assimilate carbon" (Van De Water 1993).

Climate also alters the competitive balance of species within a stand or community because species respond individually to climate change; a shift in seasonality of precipitation, for instance, will favor some species over others, and an increase in winter drought will be differentially tolerated. The amount of suitable habitat relative to different topographic, edaphic (soil-related), and microclimatic conditions also is altered by climate change so that, even though spatial distribution of plant species may be controlled by substrate, populations expand and contract as fluctuations in climate influence their sensitivity to differences in the water-holding capacity of the soil (Graumlich and Davis 1993; Prentice et al. 1991). Global temperature variation, shifts in upper atmosphere circulation patterns, and redistribution of precipitation thus have a cascading effect down to the level of community dynamics and the physiology and life history of specific individuals, which are relatively more important at that level. But changing landscape patterns at smaller timescales reflect a transition of processual dominance that makes the effects of climatic variability unclear.

Paleoecological data are often used to estimate past climatic variables. Methods range from an ecological intuition based on a combination of intimate knowledge of the vegetation distribution in an area and precipitation and temperature data from local weather stations, lapse rates, and available autecological studies of individual species to more rigorous quantitative models.

Independent models of climate change, such as the GCMs cited earlier (Webb 1986), assist in understanding how vegetation responds to complex variation in climate. Many other types of paleoenvironmental data—the relative position and dating of glacial moraines, periglacial features, past lake levels, paleosols—contribute to a more complete representation of past climates, but they are insufficient for the identification of causes because of convergence, in which different processes and causes produce similar effects, and, conversely, divergence, in which similar processes and causes produce different effects in different regions (Schumm 1991). Synoptic to global-scale model simulations, compared with paleoenvironmental data, can help identify effective processes and causes.

PALEOECOLOGICAL METHODS

As a member of the geological sciences, paleoecology uses the consequent structures of biological and physical processes to infer past system states. The two principal methods used in the Sierra Nevada study area are pollen analysis and the analysis of plant macrofossils from sediments and pack rat middens.

Pollen Analysis

The analysis of palynomorphs (including pollen, spores, and algae colonies) can provide a continuous, high-resolution vegetation chronology. Samples of pollen and spores are preferably collected with coring apparatus from stratified wet sediments in meadows, marshes, peat bogs, ponds, and lakes. Pollen is also retrieved from soils, cave sediments, spring deposits, archaeological deposits, alluvium, glacial ice, and pack rat middens. Contemporary pollen rain is sampled by a variety of traps. A sediment core or section is subsampled at intervals in the laboratory and the pollen and spores extracted and concentrated by dissolving the organic and mineral matrix with acids. The residue is mounted on slides, and the palynomorphs are identified with a binocular microscope and tabulated. Each subsample consists of an assemblage of taxa calculated in proportional or absolute terms. The assemblages are usually plotted as a pollen diagram arranged by abundances along the horizontal axis and by depth and stratigraphic age along a vertical axis (figure 4.5). Chronological control is routinely accomplished by radiocarbon-dating organic matter or humic acids in the core. By graphically displaying variation in pollen and spore abundance through time, the pollen diagram becomes the primary instrument for interpretation of vegetation changes.

The basic assumption of pollen analysis is that pollen assemblages sampled from traps or sediments directly represent vegetation composition, with correction made for differential pollen production and dispersal among plant taxa. The pollen record of a vegetation type is dependent on a system of transportation, sedimentation, and preservation of pollen grains that is a function of mesoscale topographic winds, drainage patterns, distance to a depositional basin, basin size, and depositional environment. Areas from which pollen is derived at a collection site are conventionally divided by distance into local, extralocal, regional, and long-distance.

There are three general factors that contribute to the success of pollen analysis. (1) Distinctive morphological characteristics of shape, aperture type, and surface sculpture make pollen and spores readily identifiable to family, generic, and (rarely) species taxonomic levels. (2) The small size (10–100 microns) of pollen and spores and the enormous number produced assure that they are uniformly mixed in the atmosphere and widely distributed and therefore conducive to the appli-

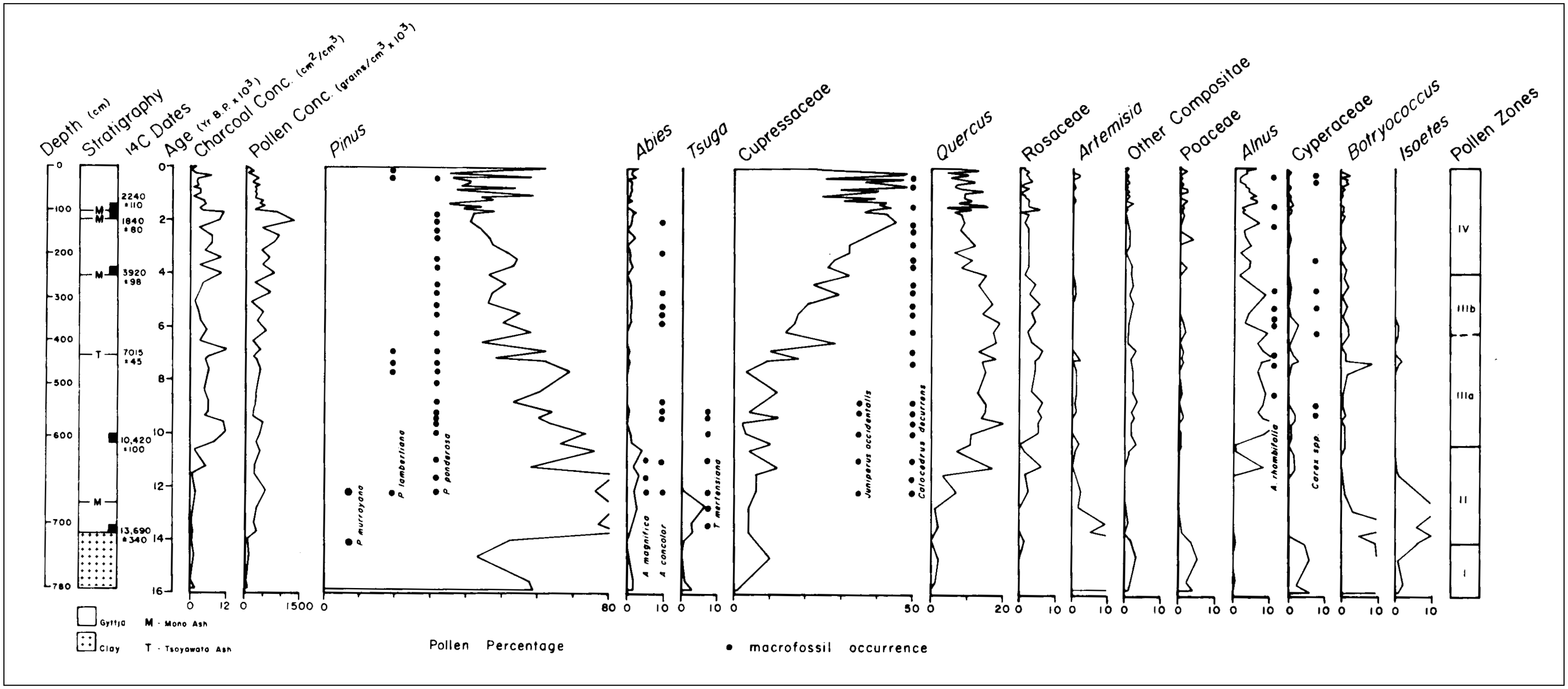


FIGURE 4.5

Summary pollen diagram with macrofossil occurrences and charcoal concentration for Swamp Lake, Yosemite National Park (from Smith and Anderson 1992).

cation of statistical methods. (3) The outer wall of most palynomorphs is made of sporopollenin, an inert organic compound highly resistant to decay. Sporopollenin is sensitive to oxidation, however, so acidic, anaerobic, permanently waterlogged environments provide the best preservation. Pollen and spores can also be mechanically and chemically damaged during transport by wind and water to the final site of deposition.

These three factors also contain biases that cause over- or underrepresentation of taxa in the database and create problems in interpretation. Pollen grains differ in their resistance to deterioration according to the amount of sporopollenin contained in the wall structure and the thickness of the wall. Populus pollen, for instance, is very thin walled and poorly preserved. Some plants produce very small amounts of pollen (Linum), whereas others (Pinus, Quercus) are very prolific. Differences in dispersal is another bias. Some pollen, especially low-production zoophilous types (dispersed by insects, birds, and bats), travel only a short distance from the source plant, whereas the more abundant and aerodynamic wind-borne (anemophilous) types, such as Pinus and Ephedra, can be carried very long distances. Pinus pollen dominates most samples from the western United States out of all proportion to the abundance of the source trees.

Macrofossil Analysis

Preserved plant parts complement the pollen and spore records. The advantage of macrofossils is that they can usually be identified to species, whereas most pollen can be identified only to the family or generic level.

The analysis of pack rat middens to reconstruct past vegetation has been successful in the deserts of western North America, where the arid climate preserves the middens and restricts the availability of wetland pollen sites. Pack rats (Neotoma spp.) gather plant material within an approximately 30–50 m foraging range around their dens (Finley 1990; Vaughan 1990). These clippings of leaves, stems, fruits, seeds, flowers, and other debris are discarded in the den to accumulate as a midden. The entire mass may eventually be sealed in an indurated matrix of crystallized rat urine to make it resistant to erosion and decay for thousands of years if protected from moisture and erosion. It is assumed that the plant parts preserved in a midden directly represent the local vegetation growing at the time the midden was accumulating. An array of radiocarbon-dated middens of various ages from a single locale will then reveal vegetation changes through time. The fundamental assumption of midden-vegetation relationship is subject to several biases, such as pack rat dietary preferences, pack rat selectivity with distance from the den, the length of time for midden deposition, and postdepositional history (Spaulding et al. 1990). Comparison of modern midden contents with vegetation growing around the dens shows that the percentage of plants common to both the midden and the local vegetation ranges between 36% and 78% (Dial and Czaplewski 1990), although in other studies similarity values range up to 89% and 92% (Cole 1983). The proportions of plant taxa in the local vegetation and in middens do not correlate reliably because of pack rat selectivity and disparities between sampling methods (Spaulding et al. 1990), but at least they reveal the presence or absence of taxa. Pack rat midden sites are restricted to the drier parts of the southern Sierra Nevada and the desert fringes of the study area, including the White-Inyo Range.

When present, plant macrofossils can also be extracted from sediments as part of a pollen analysis. They provide information on the species growing locally around the deposition site.

QUATERNARY PALEOECOLOGICAL RECORD IN THE STUDY AREA

Pollen studies have significantly increased in the Sierra Nevada study area over the past decade. Since the pioneering work by David Adam (1967) on a core from Osgood Swamp and three stratigraphic sections from Yosemite National Park, over fifty published and unpublished pollen profiles have been compiled, not counting records from archaeological deposits (see appendix 4.1). Most sites are located in the central western Sierra Nevada and Lake Tahoe Basin subregions and the very northern part of the southern Sierra Nevada subregion, between elevations of 1,510 m (4,950 ft) and 3,020 m (9,900 ft) (figure 4.6). Quality varies from deep stratigraphies to short segments taken from archaeological sites. The few pack rat midden sites studied so far are located in Kings Canyon, the White Mountains, Owens Valley, and the Scodie Mountains, the driest parts of the SNEP study area. Almost all of the pollen and midden sites together date from the middle of the last glaciation (40,000 years ago), and most record only the past 10,000–12,000 years. Accordingly, this narrative of Quaternary vegetation history will be subdivided into time periods appropriate to the detail of available information. It is important to note that descriptions of vegetation changes may not conform to time period boundaries, because a regionally coherent vegetation response to a climatic transition, for instance, will occur at different times according to elevation and latitude. Plant nomenclature follows The Jepson Manual (Hickman 1993), and vegetation types are, for the most part, taken from Barbour and Major (1990).

Early Pleistocene (2.4–1.0 Ma)

Only seven pollen records date to the early Pleistocene (2.4–1.0 Ma), felicitously located at both ends and in the middle of the study area. Five of the records are in the vicinity of the southern Sierra Nevada subregion (Axelrod and Ting 1962). They are not chronologies but discrete pollen assemblages (termed “floras” by Axelrod) from sedimentary units repre-

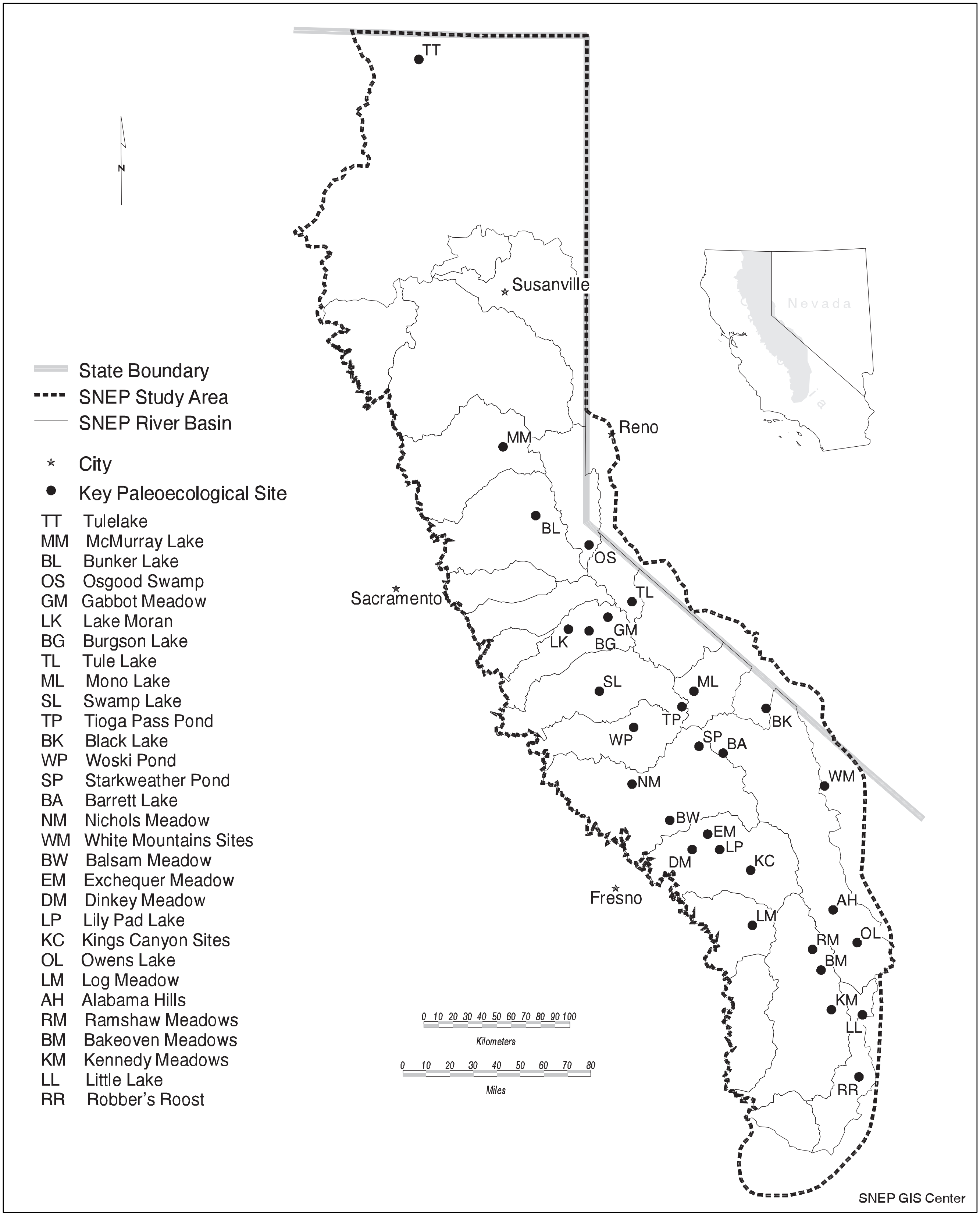


FIGURE 4.6

Map of key paleoecological sites in the SNEP study area.

senting a single depositional episode. Almost all of the pollen has been identified to species, a level of taxonomic resolution not usually attained by Quaternary palynologists. Analyses were done by sorting the species into groups resembling modern plant communities, placing the site into the most likely community, and then estimating the elevation and climate during the time of deposition. Finally, the sites were dated according to the composition of the taxa relative to other dated pollen assemblages and the available geological evidence.

Southern and East-Side Sierra Nevada

A north-to-south sequence of three pollen assemblages was recovered from exposed sediments at Ramshaw Meadows, Bakeoven Meadows, and Kennedy Meadows on the Kern Plateau. The other two assemblages were taken from road cuts through the Alabama Hills in the Owens Valley and farther south near Little Lake in Rose Valley. Axelrod interpreted the assemblages to be representative of the modern upper yellow pine (white fir–mixed conifer) forest of northern California and southern Oregon, with red fir and subalpine communities growing at higher elevations. This geographic placement is due to the presence of pollen identified as Abies grandis (grand fir), Tsuga heterophylla (western hemlock), Cupressus lawsoniana (Port Orford cedar), Taxus brevifolia (Pacific yew), Pseudotsuga menziesii (Douglas fir), Lithocarpus densiflora (tan oak), Acer circinatum (vine maple), and Myrica hartwegii (Sierra sweet bay) (some names have been changed in accordance with modern nomenclature). These species now grow farther north in the Sierra Nevada and the Cascades and along the coast. A latitudinal and elevational gradient is inferred from a decrease in the abundance of these humid species from Ramshaw Meadows to Little Lake. The abundance of Pinus longaeva (bristlecone pine) pollen from the Owens Valley and Little Lake sites led Axelrod to postulate that this species was also a component of the yellow pine forest during the early Pleistocene.

According to Axelrod, these pollen assemblages are indicative of a climate cooler and wetter than at present. The apparent absence of alpine, piñon woodland, sagebrush, and warm desert scrub taxa points to a later regional occupation of these vegetation types. Elevations were apparently lower, with little difference in relief between the depositional basins; the Sierra Nevada rain shadow was not climatically effective, and the Owens and Rose Valley grabens had not yet dropped. Because of the moderate topography and the lack of pollen from the Tertiary (a geologic period dating between 65 and 2.4 Ma), Axelrod dates the southern Sierra Nevada pollen assemblages to the early Pleistocene, after the initial uplift of the mountain range and at the inception of alpine glaciation (the McGee) between 2 and 3 million years ago.

Recent work on the tectonic history of the Sierra Nevada, however, estimates the initiation of significant uplift and westward tilting between 25 and 10 million years ago, in the late Miocene or Pliocene (Huber 1981). Uplift accelerated until the range essentially achieved more than 80% of its present height during the early Pleistocene. Further, subsidence of Owens Valley is estimated to have begun during the early Pliocene, 5–6 million years ago (Bacon et al. 1979; Giovanetti 1979) and the 3-million-year-old lake beds of the Coso Formation give evidence that Rose Valley was depressed by that time (Duffield et al. 1980). In light of this, if Axelrod's vegetation reconstruction is correct, the Kern Plateau and Owens Valley pollen assemblages may be mid-Pliocene in age or at least greater than 3 million years old, rather than late Pleistocene.

Lake Tahoe Basin

Another pollen assemblage from a short-term sedimentary event was recovered from a clayey silt deposit beneath a latite flow located on the north side of the Truckee River west of Tahoe City, dated by the potassium-argon (K-Ar) technique to 1.9 million years (Adam 1973). The dating of the volcanic rock provides only a minimum; the sediments could be older. The present vegetation in the area (1,900 m [6,230 ft]) is a mixed conifer forest. The fossil pollen is equivalent to modern pollen samples taken 300 m (980 ft) lower on the west slope. There are higher percentages of TCT (undifferentiated Taxaceae-Cuppressaceae-Taxodiaceae taxa, probably mostly Libocedrus decurrens [incense cedar]), Chenopodiaceae-Amaranthus (usually abbreviated by pollen analysts to Cheno-Ams), Artemisia (sagebrush), and Poaceae (grass) pollen and lower percentages of Abies (fir), Quercus (oak), and Asteraceae pollen, compared with a modern surface sample taken from near the fossil site. This difference may indicate a period of slightly drier or warmer conditions in the early Pleistocene except for the presence of fossil Picea (spruce) pollen. Today the nearest population of Picea is at Clark Creek, about 240 km (150 mi) northwest of Tahoe City, where there is adequate warm-season precipitation. Picea is apparently restricted by a summer moisture deficiency longer than two or three months (Adam 1973).

Modoc Plateau

The longest pollen record in the SNEP study area is from Tulelake Basin (Adam et al. 1990; Adam et al. 1989). This remnant Pleistocene lake is immediately east of Lower Klamath Lake on the Modoc Plateau. The rain shadow effect of the southern Cascade Range maintains a sagebrush steppe around the basin. At higher elevations to the west, plant communities include ponderosa pine–bitterbrush shrub forest, mixed conifer forest, and upper montane–subalpine forest. In more xeric (low-moisture) sites at higher elevations to the east are manzanita-Ceanothus chaparral and juniper-sagebrush steppe woodlands.

The bottom of the 334 m (1,096 ft) sediment core retrieved from the basin is dated to 3 million years. The published pollen diagram presents only the most abundant taxa, including Pinus, Quercus, and TCT (probably mostly Juniperus occidentalis and *Calocedrus decurrens*); Artemisia, other

Asteraceae (composites), Cheno-Ams, and Sarcobatus (greasewood); and Poaceae and Cyperaceae (sedge and tule). Whereas these pollen types represent the surrounding terrestrial and lakeside vegetation, the presence of algae colonies and diatoms in the sediments reflects a lacustrine environment. The pollen is used by the authors primarily as a climatic record; interpretation in terms of vegetation is minimal, and the time resolution is low.

Proportional variations among these pollen taxa record changes in forest and woodland, desert, and valley bottom vegetation as they respond to climate change. Adam interprets the high percentages of Pinus and TCT pollen (along with temperature- and chemistry-sensitive diatom taxa) during the termination of the Pliocene as extensive coniferous forest around a warm, shallow, slowly drying lake. When the low percentages of Artemisia and Cheno-Ams pollen are also taken into account, the climate can be inferred to be more humid than it is today, although there were dry periods. At the beginning of the Pleistocene the pollen curves change from lower (smoother) to higher (spikier) frequency variation, the amplitude of TCT pollen decreases slightly, and Artemisia pollen becomes more abundant. An appreciable drying trend began after 1.64 million years, as indicated by a decrease in TCT pollen and coextensive increase in Artemisia, Asteraceae, Poaceae, and Cheno-Ams, along with intervals of lake desiccation. The vegetation was apparently responding to both the dryer, colder glacial climates and the increasing rain shadow as the Cascades were uplifted. The coniferous forest seems to have been opening up, and sagebrush steppe was becoming more prevalent.

Late Pleistocene (1.0 Ma–10 ka)

Modoc Plateau

The Pleistocene vegetation trends in the Tulelake Basin core continue after 1 million years with a significant decrease in TCT pollen, and Artemisia, other Asteraceae, Cheno-Ams, and Poaceae increase to the highest percentages in the core. Inverse fluctuations between pine and juniper-type pollen indicate glacial cycles imposed on the overall drying trend as the modern sagebrush steppe is established. Quercus pollen shows no definite trend throughout the core, but it varies in concert with TCT pollen and provides a similar signal of glacial cycles.

East-Side Sierra Nevada

The only other pollen record within the SNEP study area that spans nearly the past million years comes from Owens Lake (Litwin et al. 1995). A 323 m (1,060 ft) core recovered from the lake sediments extends back to about 800,000 years, based on the presence of the Brunhes-Matuyama magnetic-reversal boundary (780 ka) and Bishop ash (760 ka) near the bottom (Owens Lake Core Study Team 1995).

Modern vegetation surrounding Owens Lake is zoned by elevation into saltbush-greasewood scrub on the valley bottom and lake basin; creosote bush scrub, shadscale and blackbush mixed-desert scrub, and sagebrush scrub on the alluvial fans; piñon or piñon-juniper woodland above that; and upper montane, subalpine forests, and alpine communities along the crest. Riparian vegetation consists of tree and shrub forms of Salix spp. (willow), Populus fremontii, P. angustifolia, and P. trichocarpa (cottonwood), with Populus tremuloides (aspen) at higher elevations. Small stands of Quercus kelloggii (black oak) and Q. chrysolepis (canyon live oak) also grow along the drainages of the eastern escarpment.

The preliminary Owens Lake pollen diagram for the entire core has a very coarse resolution of about 5,900-year sampling intervals. General patterns of glacial cycles, however, are discernible in the inverse relation of pine and juniper pollen: as climate went into a glacial phase, Juniperus increased and Pinus decreased. Another clear periodicity is an increase in Artemisia that precedes Juniperus with the beginning of each glaciation. Long-term trends are the increase in peak abundances of juniper pollen and a slight increase in Quercus and Salix. The other taxa show no trends throughout the core.

The interval of 800,000 to about 685,000 years ago at the bottom of the core is distinguished by relatively high percentages of Abies and Picea and low percentages of Juniperus. Abies attains similar values in the upper part of the core, but Picea is only occasionally present. Picea is an anomaly. The only other place it has been identified in Sierra Nevada Quaternary sediments is in the Tahoe City assemblage (discussed earlier). It is more likely to have grown in the northern Sierra Nevada during the early Pleistocene than in the more xeric southern end of the range, even during the full glacial periods. It was not identified in the Tulelake core, although there are populations of two species (Picea engelmanii and P. breweriana) in restricted areas to the southwest and in the Siskiyou and Klamath Mountains (Griffin and Critchfield 1972). The characteristics of Picea pollen are distinctive enough not to be confused with Pinus, if preservation is good, so errors in identification are minimal. Picea pollen is very buoyant like Pinus, although nearly four times heavier and with twice as much settling velocity (Erdtman 1969), so it will not travel as far. It has been reported as a component of the modern pollen rain from Pleistocene Searles Lake, about 37 km (60 mi) southeast of the Owens Lake coring site (Leopold 1967). The nearest Picea populations today are in northern Arizona mountains. The pollen may have been brought into southeastern California by expanded monsoonal flow during the height of the interglacials because most of the peaks of Picea pollen coincide with periods of high Pinus and low Juniperus, which mark the interglacials.

Another anomalous pollen type found occasionally throughout the Owens Lake core is Juglans (walnut). A small stand now growing in Owens Valley may have been planted in historic times. The habitat of Juglans hindsii, historically present along the Sacramento River and near the delta, and J. californica in the southern California coastal mountains has a strong marine influence with small seasonal temperature variations, unlike the more continental regime of the eastern Sierra Nevada. It is more likely that the Juglans pollen of Owens Lake represents a northward expansion of J. major (Arizona black walnut) during the Pleistocene.

A finer-resolution (670-year intervals) pollen record from Owens Lake is being compiled for the past 150,000 years (Woolfenden 1995). This interval covers the last two major glacial cycles. As the record is interpreted so far, there was a general increase in Utah juniper (Juniperus osteosperma) woodland on the alluvial fans of the Sierra Nevada and Inyo Mountains and probably around the lake margins throughout the last glacial (Tioga) from about 73,000 to a maximum at about 20,000 yr B.P. Pinus monophylla (singleleaf piñon) and other white pine pollen have higher percentages than yellow pine pollen during this period. Most of the white pine pollen may represent the expansion of Pinus longaeva (bristlecone pine) and P. flexilis (limber pine) subalpine forests in the Inyo Mountains and the depression of the elevational range of P. monticola (western white pine), P. balfouriana (foxtail pine), P. flexilis, and perhaps P. albicaulis (whitebark pine) lower on the Sierra Nevada escarpment. Species such as P. contorta (lodgepole pine) and P. jeffreyi (Jeffrey pine) and other elements of the upper montane forest (red fir, white fir, and mountain juniper) were probably included in the forest. A component of Pinus pollen may have blown over from the west slopes. The increase in P. monophylla pollen indicates a lowering of the elevational limits of this species on the rockier portions of the bajadas as an associate of juniper, and possibly an increase in its density on the desert mountains to the south. These trends, along with the concomitant increase in Artemisia pollen, and higher percentages of Poaceae (signaling the expansion of sagebrush steppe) suggest a transition to a climate cooler and wetter than today's. The termination of the Tioga glaciation at about 14,000 years ago is represented by a decrease in juniper relative to pine and an increase in Ambrosia cf. dumosa (white bursage), Cheno-Ams, and Cercocarpus-Purshia (a type of Rosaceae pollen undifferentiated among Cercocarpus ledifolius [mountain mahogany], Purshia tridentata [bitterbrush], and Coleogyne ramosissima [blackbush]). The trend in shrub taxa indicates a spread of warm-desert species in the Owens Lake Basin. The warm and subhumid waning stages of the last interglacial, between about 110,000 to 75,000 years ago, is similarly reflected by high percentages of Abies—probably Abies concolor (white fir) and A. magnifica (red fir)—Pinus, Cheno-Ams, Cercocarpus-Purshia, and Ambrosia types.

Two pack rat middens collected on the northeast side of Owens Lake, 10 m (33 ft) above the highest Pleistocene lake level (1,145 m [3,757 ft]) provide evidence for the floral characteristics of lakeside vegetation between 22,900 and 14,870 yr B.P. (Koehler and Anderson 1994a). The vegetation around the site is at present a mixed shadscale-sagebrush scrub with nearby creosote bush–bursage (Larrea tridentata–Ambrosia dumosa) communities on the fans. The full- to late-glacial midden macrofossils are typical of a Utah juniper–singleleaf piñon woodland with an understory of xeric shrubs, cactus, and grasses such as Ericameria cuneata (cliff goldenbush), Ephedra viridis (green joint fir), Menodora spinescens, Glossopetalon spinescens (Nevada greasewood), Opuntia basilaris (beavertail cactus), and Achnatherum hymenoides (Indian ricegrass), among others. The unusual find of Juniperus scopulorum (Rocky Mountain juniper) in midden layers dating 20,590 and 16,010 yr B.P. is the first observation of this species west of its present westernmost location in the Charleston Mountains of southwestern Nevada. Its Pleistocene occurrence around Owens Lake may be due to high water tables or the moderating influence of the expanded lake on local climate. Pollen extracted from the midden samples reflects the macrofossil assemblage except for a high abundance of Artemisia pollen.

North of Owens Lake, a spectacular 31,500-year sequence of twenty pack rat middens was recovered from the Alabama Hills on three sites with southern exposures (Koehler and Anderson 1995). The macrofossils and pollen contained in the middens are congruent with the Owens Lake pollen record and further enhance the late Pleistocene vegetation history of the eastern Sierra Nevada. During the middle- to full-glacial interval from 31,450 to 20,310 yr B.P. a Utah juniper–Joshua tree (Yucca brevifolia) community with an understory of Artemisia tridentata, Purshia tridentata, and Atriplex confertifolia (shadscale) grew in the Alabama Hills. The association of Yucca brevifolia with Juniperus osteosperma has not been described and may not have a modern analog, although its association with Juniperus californica (California juniper) is known in the Mojave Desert (Vasek and Thorne 1990). As with Juniperus scopulorum on the eastern shore of Owens Lake, Yucca brevifolia may signal a moderate local glacial climate influenced by an expanded lake, with winter temperatures not much lower than in recent times. Artemisia and Purshia tridentata, however, imply cooler summers.

Around 19,070 yr B.P. climatically significant changes occurred with the appearance of the more xeric shrub species Ericameria cuneata and Purshia mexicana (cliffrose) and the departure of bitterbrush. Joshua trees disappeared by 17,760 yr B.P., followed by the departure of Rocky Mountain juniper and the upslope retreat of piñon from the shores of Owens Lake by 16,010 yr B.P. (Koehler and Anderson 1994a). The apparent warming and drying trend continued between 13,350 yr B.P. and 9540 yr B.P. with the arrival of blackbush, Opuntia echinocarpa (cholla), and Lycium andersonii (wolfberry) and the local departure of Juniperus osteosperma soon after that.

Late glacial woodland is also documented at the southern end of the Sierra Nevada (McCarten and Van Devender 1988). Three pack rat macrofossil assemblages dated at 13,800 to 12,820 yr B.P. from the 1,125 m (3,690 ft) elevation Robber's Roost site in the Scodie Mountains are dominated by Pinus monophylla, Juniperus californica, Ceanothus greggii, Artemisia tridentata, Purshia tridentata var. glandulosa (desert bitterbrush), Quercus turbinella, and Yucca brevifolia. The best analog for the assemblage is not the piñon-oak woodland 600 m (1,970 ft) just above the midden site (which is composed of Pinus monophylla, P. sabiniana, and Quercus chrysolepis) but piñon-juniper woodland on the north slope of the San Bernardino Mountains. The modern vegetation aound the Robber's Roost site is a creosote bush–bursage scrub.

McCarten and Van Devender make an important point about the macrofossils at Robber's Roost that can be extended to the Alabama Hills middens. Even though these midden sites are located near the base of the eastern escarpment of the Sierra Nevada, the fossil plant assemblages do not contain Sierran montane trees that should have dispersed east into the Alabama Hills or south and east into the Scodie Mountains.

Farther north, eight pack rat middens recovered from the White Mountains and Volcanic Tablelands afforded a chronological sequence of past vegetation at six disjunct locales between 19,290 yr B.P. and 2130 yr B.P. (Jennings and Elliott-Fisk 1993). The two earliest-dated middens, from adjacent Volcanic Tablelands sites (1,341 m [4,400 ft]), span the interval from the full-glacial to the opening of the Holocene. The modern vegetation is a mixed shadscale and sagebrush scrub. Plant macrofossils of one midden show that an entirely different plant community existed 19,000 years ago. At that time Utah juniper, in association with Purshia tridentata var. glandulosa (desert bitterbrush), Tetradymia axillaris (cottonthorn), T. canescens (horsebrush), and Ericameria cuneata, among other species, grew around the site about 600 m (1,970 ft) below the present lower border of piñon-juniper woodland. More than 9,000 years later, as revealed by the second midden, radiocarbon-dated to 9830 yr B.P., Juniperus osteosperma and Purshia tridentata var. glandulosa were still in the area, but the other shrub associates were replaced by Chamaebatiaria millifolium (fernbush), Prunus andersonii (desert peach), Ribes velutinum (gooseberry), and Artemisia spp. This shift in the flora is among species now occupying shared elevation ranges on dry slopes (or, in the case of Ribes velutinum, moist and shaded habitats) in the White Mountains and does not necessarily signify climate change.

An 11,500-year core taken from the west side of Mono Lake contains a pollen record typical of a late-glacial Great Basin juniper-sagebrush woodland (Davis 1993). Today Pinus monophylla grows on the lower slopes above the lake, with a sagebrush-bitterbrush understory. There are stands of Juniperus osteosperma to the east on the north side of the lake. Pinus jeffreyi occupies the drainages. An unusual feature is the high percentage of Sequoiadendron pollen in the 11,500–10,000 yr B.P. interval, up to 20% near the base of the core. Studies of Sequoiadendron pollen dispersal at Lost Grove and Tuolumne Grove have determined that this pollen type is not widely dispersed outside the groves (Anderson 1990b). Percentages drop to about 20% at about 100 m from the edge of the groves and less than 5% within 500 m of the grove. Therefore, it is possible, although a biogeographical anomaly, that the Sequoiadendron pollen in Mono Lake came from nearby stands of Sequoiadendron giganteum (giant sequoia).

A pollen record from Tule Lake (2,080 m [6,820 ft]), at the base of the escarpment east of Sonora Pass, is undated, but time periods can be generally inferred from changes in the proportions of pollen taxa (Byrne et al. 1979). Present vegetation is sagebrush-bitterbrush scrub with open stands of Pinus jeffreyi, Juniperus osteosperma, and Cercocarpus ledifolius on the surrounding ridges. The lake is located behind a Tioga-age terminal moraine that gives a minimal deglaciation date for the vegetation record of about 14,000 yr B.P. The lower two-thirds of the pollen profile is dominated by Pinus, TCT (Juniperus), and Artemisia pollen. This probably represents a cold-dry late-Pleistocene juniper woodland with associated pine.

Just east of the Sierra Nevada crest, a high-elevation pollen record was taken from Barrett Lake (2,816 m [9,240 ft]). It is situated within the mixed mountain hemlock–red fir–lodgepole pine–limber pine forest. The pollen spectra in the 11,730–10,000 yr B.P. interval is similar to modern samples from open subalpine forest and at tree line. In addition to the lack of macrofossils in the lake sediments and very low pollen concentrations, this implies a near-treeless newly deglaciated landscape (Anderson 1987).

West-Slope Sierra Nevada

Unlike east-side Sierra Nevada and northeastern California, where the availability of deep Pleistocene lake basins and pack rat midden sites allows for extended vegetation chronologies well back into the Quaternary period, the western slope of the Sierra Nevada has produced continuous vegetation histories only since the Tioga glacial maximum (18,000–20,000 yr B.P.). (Two exceptions are discussed later.) The shorter chronologies are a consequence of the scarcity of natural lakes and wetlands at elevations below the glacial termini and conditions arid enough for the preservation of pack rat middens. Another reason may be a deficiency of fieldwork intensive enough to discover deeper sediments and middens. Before global deglaciation was initiated sometime after 17,000 years ago (Fairbanks 1989), and at least 15,000 years ago in the Sierra Nevada (Byrne et al. 1993), the 430 km (267 mi) ice cap–mountain glacier complex covered and was scouring what were to become pollen sites. The ice cap itself was limited by the balance between winter snow accumulation and summer melting. This annual snowline or equilibrium line altitude (ELA) on southern aspects ranged from about 2,400 m (8,000 ft) in the northern Sierra Nevada to about 4,000 m (13,000 ft) in the southern Sierra Nevada (Porter et al. 1983; Wahrhaftig and Birman 1965). Above an average of about 2,500 m (8,200 ft), valley glaciers fed mid-altitude ice fields created when glaciers overtopped canyon divides and coalesced. Below 1,800 m (5,900 ft) in the central Sierra Nevada, the ice fields fed valley glaciers that descended farther than 60 km (37 mi) down west-slope canyons to about 600–1,200 m (1,970–3,940 ft). On the steeper eastern escarpment, valley glaciers descended 15–27 km (9–17 mi) to elevations between 1,300 and 2,200 m (4,260–7,220 ft). It is clear that the basins from which upper-elevation pollen records were retrieved were within reach of glaciers or that the high velocity of glacial meltwater streams prevented the accumulation of deep sediments.

The single pack rat midden record from the cismontane Sierra Nevada is a sequence of eight samples of four middens recovered from caves in lower Kings Canyon at an elevation range of 920–1,270 m (3,020–4,170 ft) and dating to a late Pleistocene time interval of greater than 40,000 yr B.P. to 12,500 yr B.P. (Cole 1983). The present vegetation type is oak–pine / chaparral woodland of Quercus chrysolepis and Pinus monophylla with an understory dominated by Cercocarpus betuloides (birch leaf mountain mahogany), Cercis occidentalis (western redbud), Umbellularia californica (California bay), Garrya flavescens (silk tassel), Ceanothus integerrimus (deer brush), Yucca whipplei (Our Lord's candle), Rhamnus crocea (spiny redberry), and Elymus trachycaulus spp. subsecundum (slender wheatgrass). The major difference between modern and midden-based Pleistocene floras is the past absence of Quercus and several xeric shrub and wheatgrass associates in middens and the presence of a very diverse mixed conifer forest during glacial times. Throughout nearly 26,000 years since 40,000 yr B.P., Kings Canyon was occupied predominantly by Juniperus occidentalis associated with Abies grandis, Calocedrus decurrans (incense cedar), Pinus lambertiana (sugar pine), P. cf. ponderosa (yellow pine), and a single occurrence (17,520 yr B.P.) of Torreya californica (California nutmeg). Juniperus macrofossils were most abundant in the sample dated to 20,000 yr B.P. Pinus lambertiana departed by 14,600 yr B.P., Abies grandis by 14,190 yr B.P., *Calocedrus decurrens* by 12,500 yr B.P., and Juniperus occidentalis and yellow pine after 12,500 yr B.P. Pinus monophylla was present throughout most of the interval to the present day.

Species common to Pleistocene and modern vegetation communities are Pinus monophylla, Ceanothus integerrimus, and Garrya flavescens. Sequoiadendron pollen extracted from the middens implies the presence of Sequoiadendron giganteum closer to the sites than the modern groves. Except for Abies grandis, *Calocedrus decurrens*, Torreya californica, and Sequoiadendron giganteum, which probably inhabited nearby shaded ravines, the composition of the Pleistocene forest is more typical of the east side than the present west-slope montane forest at higher elevations. Cole attributes this either to the marble substrate of the Kings Canyon sites, or to a cold, dry late-Pleistocene climate across the continent, or to a combination of both, with an uneven snow accumulation maintaining the mesic species (those requiring a moderate amount of moisture).

A relatively xeric late-Tioga glacial climate with a local, irregular distribution of water availability is demonstrated by cores taken from Tulare Lake in the southern San Joaquin Valley (Atwater et al. 1986; West et al. 1991). Pollen abundances show high Juniperus, Artemisia, Sarcobatus, and Sequoiadendron from about 26,000 yr B.P. to about 13,000-11,000 yr B.P. From this evidence Sequoiadendron giganteum was inferred to be more widespread and probably a component of an extended riparian woodland along the Kern River into the San Joaquin Valley. The pollen is now thought to have been transported downriver during flood events.

West-slope pollen and macrofossil stratigraphies document a consistent pattern of vegetation-climate change in the central and southern Sierra Nevada subregions, although timing and floristic details differ among sites according to latitude and elevation. The earliest of these pollen profiles, dating well into the late glacial, are from intermediate elevations, below 2,500 m (8,200 ft) in the lower and upper montane forests.

At present, Nichols Meadow provides the only full-glacial (about 18,500 yr B.P.) pollen spectra (Koehler and Anderson 1994b). The meadow is located within the Nelder Giant Sequoia Grove in the Fresno River drainage basin at an elevation of 1,510 m (4,950 ft). It is the lowest pollen site in the Sierra Nevada, near the upper margin of the ponderosa pine forest and the lower margin of the white fir–mixed conifer forest. The pollen spectra at the base of the core represent an open sagebrush-grass community or perhaps a woodland with scattered white and yellow pine and Juniperus nearby. This is indicated by very high percentages of Artemisia and Poaceae with relatively significant amounts of Pinus and Cupressaceae based on a very low pollen influx, which means the tree pollen came from a distant source or from a very few individuals in the area. Herb pollen is also common. The ratio of sagebrush to grass is equivalent to that of the late glacial sequences of the northern Rocky Mountains of Wyoming, southwestern Montana, and southeastern Idaho, and modern sagebrush steppe in the basins of northeast Wyoming (Baker 1983). The pollen spectra also resemble those of modern Sierra Nevada alpine communities east of the crest. Both reflect a cold, dry periglacial climate. The community persisted at Nichols Meadow until 12,500 yr B.P.

A subalpine sagebrush steppe–woodland, represented by high frequencies of Artemisia and (in some central Sierra Nevada sites) Juniperus and Sarcobatus pollen is recorded at other sites above 1,500 m, where the modern vegetation is montane forest.[1] This pollen zone dates from the base of the cores, between 16,000 and 11,000 yr B.P., and continues until 13,000–10,000 yr B.P., depending on elevation and latitude. It seems to have persisted into the early Holocene, until about 7000 yr B.P., at Balsam and Exchequer Meadows in the more xeric southern Sierra Nevada. Also, between 16,000 and 11,000 yr B.P., change in the hydrology is seen in a transition of the basal sediments from gravels, sands, silts, and glacial flour to organic silts, muds, and peat.

Variation in the proportions of pollen types shows that sagebrush steppe was replaced relatively rapidly by a closed conifer forest as the climate became warmer, with more effective moisture. Within about 500 years, percentages of Pinus and Abies increased as Artemisia, Poaceae, and herb pollen decreased. Pinus, especially, reached maximum values for the entire late Quaternary record.

Evidence for trees colonizing the sites is the higher percentages of arboreal pollen and the presence of macrofossils. Conifers are identified to species in the few analyses that included macrofossils. Abies concolor, Pinus lambertiana, Pinus ponderosa-type, Calocedrus decurrens, and Sequoiadendron grew around Nichols Meadow. The forest at the higher Lake Moran site from 12,000 to 10,000 yr B.P. was composed of Pinus lambertiana, P. monticola, P. contorta, and some Tsuga mertensiana. Pinus lambertiana and Abies concolor were two species at Bunker Lake.

Similar to that of the Kings Canyon macrofossil assemblage, a very diverse forest of lower and upper montane and subalpine species was established at Swamp Lake, Yosemite National Park (YNP), after 13,700 yr B.P. and remained for about 3,300 years. Lodgepole pine, western white pine, ponderosa pine, white and red fir, incense cedar, mountain hemlock, and western juniper provided the species mix. Smith and Anderson (1992) conjecture that the upper-elevation conifers may have lagged behind in suitable microhabitats as the other trees followed the changing climate upslope and that development of a more extreme seasonality of cooler, wetter winters and warmer summers created a greater variety of habitats. The species composition at some of these paleoecological sites does not resemble any assemblage in present Sierran forest. Byrne et al. (1993) make a striking conjecture, based on pollen abundance, low frequencies of Quercus pollen, and relatively low charcoal abundance, that the late-glacial dense conifer forests had a structure similar to modern mixed conifer forests conditioned by historic fire suppression.

The steppe-forest transition took place later, after 10,000 yr B.P. at Starkweather Pond and also at Gabbott Meadow, located at 1,995 m (6,550 ft) deep into the Stanislaus River drainage basin (Mackey and Sullivan 1991). A brief maximum of Abies pollen percentages, accompanied by A. concolor and A. grandis macrofossils, by about 10,000 yr B.P. reveals a slight lag in arrival of these species at the site.

Meadows developed during this period. The deposition of organic-rich sediments, along with pollen of Brassicaceae, Cyperaceae (Carex), Asteraceae, and Oxypolis (its first appearance), is interpreted to signal the inception of a small meadow after 12,500 yr B.P. at Nichols Meadow (Koehler and Anderson 1994b). Similarly, after the same date, meadow conditions appear to have been established at Lake Moran until about 10,000 yr B.P. (Edlund and Byrne 1991). The evidence is a stratum of peaty sediments and a high percentage of pollen associated with meadows: Apiaceae, Liliaceae, Onagraceae, Malvaceae, and Ranunculaceae.

This cool-wet interval is marked by the high stands of pluvial lakes in southwestern deserts between 15,000 and 12,000 yr B.P. and by the maintenance of marsh and pond conditions in some Mojave Desert valleys (Benson et al. 1990; Enzel et al. 1992; Quade 1986; Wells et al. 1987). Lakes and vegetation were apparently responding to changing atmospheric circulation and water budgets over the entire region throughout deglaciation, coinciding with the northward movement of the jet stream.

Early Holocene (10–6 ka)

From 18,000 years ago average insolation over the Northern Hemisphere is computed to have increased in the summer to a July maximum of 8% higher than today's values and decreased in the winter to a January minimum of about 8% lower than today's values by 9,000 years ago (COHMAP Members 1988) (figure 4.3). The first stages of summer warming and its effect on Sierra Nevada vegetation is reflected in the pollen records discussed earlier. With an intensification of warming came a decrease in effective moisture, and the postglacial montane forests began to change rapidly. At several sites lake levels dropped, and meadows dried and were invaded by conifers (Anderson 1990a; Koehler and Anderson 1995; Wood 1975). Tree-ring dating of the remains of bristlecone pine above the present tree line on Sheep Mountain in the White Mountains has determined that the minimum altitude of the upper tree line was up to 150 m above the present tree line prior to 3,750 years ago due primarily to higher temperatures (LaMarche 1973).

West-Slope Sierra Nevada

Under a warm, dry early Holocene climate, central Sierra Nevada sites show a decrease in Pinus and an increase in Cupressaceae (Juniperus and *Calocedrus decurrens*), Artemisia, Quercus, Alnus, Pteridiam, and herb pollen. Quercus pollen, especially, reaches its peak frequencies during this period, exceeding modern values at several sites. Abies pollen also decreases after a brief, early rise in abundance. An important correlative to shifts in proportions of pollen taxa is the dramatic increase in fire frequency as indicated by high concentrations of charcoal. It is obvious that both aridity and intensification of the fire regime were opening up the denser late Pleistocene forest canopy and changing its composition. Macrofossils provide more details. Although Pinus ponderosa macrofossils were present at low elevations in Nichols Lake and Swamp Lake YNP sediments prior to 10,000 yr B.P., the species first appeared after this date farther upslope at Lake Moran and Bunker Lake, while Pinus monticola, P. lambertiana, and P. contorta macrofossils temporarily disappeared at Lake Moran. Mesic upper-montane and subalpine species—P. contorta, Abies grandis, Tsuga mertensiana, and Juniperus—permanently dropped out of the macrofossil records at Swamp Lake YNP.

Pollen and macrofossils from Log Meadow, in the Giant Forest of Sequoia National Park (2,948 m [6,720 ft]), records a mixed conifer forest between 10,500 and 9000 yr B.P., with an absence of Sequoiadendron (Anderson 1994). After 9000 yr B.P. a few individuals of Sequoiadendron first began to grow in proximity to the site.

High-altitude forests were already in existence after the beginning of the Holocene warm period. Macrofossils of western white pine, lodgepole pine, western juniper, and red fir appear in the sediments of Starkweather Pond at about 9300, 8500, 7300, and 6300 yr B.P., respectively. These are the associates of the modern upper montane forest in the area. An open-canopy forest structure is inferred from the abundant montane shrub pollen, such as Cercocarpus, Ericaceae (probably Arctostaphylos), Chrysolepis, and probably Quercus vaccinifolia (Anderson 1990a). The shrubs, the temporary decrease and disappearance of Tsuga mertensiana pollen, and the increase in charcoal frequency are all indications of early Holocene aridity.

The highest pollen site sampled so far is Tioga Pass Pond at 3,018 m (9,901 ft) (Anderson 1987, 1990a). It is situated in a subalpine forest of Pinus contorta, associated with a few P. monticola and P. albicaulis (whitebark pine). The pollen record begins about 9300 yr B.P. with a typical assemblage of an alpine sagebrush steppe. Trees were not growing around the pond but may have been scattered in the area.

As noted earlier, the two southern pollen sites, Exchequer and Balsam Meadows, have an early Holocene vegetation record similar to that of the high-altitude sites but resulting more from aridity than an elevational lag effect. Trees were not established around the meadows until about 7500 yr B.P. Before that date an open sagebrush steppe with local stands of Pinus, Abies, and Juniperus or *Calocedrus decurrens* apparently persisted from the late-glacial. The longer Exchequer Meadow record shows a decrease in Artemisia and Poaceae pollen from the higher abundances between 13,500 and 11,000 yr B.P. After 10,000 yr B.P., conditions remained fairly constant at Balsam Meadow, while a gradual trend in nearby forest development is evident at the higher-elevation Exchequer Meadow. There, Pinus and Abies pollen steadily increased throughout the interval to 7000 yr B.P. Quercus pollen also became more frequent in the Exchequer Meadow sediments between about 10,000 and 7000 yr B.P., and the abundance of Sequoiadendron pollen, centered at 10,680 yr B.P., indicates an extension of the upper-elevation range of that species.

East-Side Sierra Nevada

A lodgepole pine–limber pine forest is inferred to have been established at Barrett Lake by 10,000 yr B.P., followed by local individuals of Tsuga mertensiana a thousand years later. There is then no discernible trend in conifer pollen between 10,000 and 6000 yr B.P. except for a slight increase in mountain hemlock. Shrub pollen representing east-side mountain and basin vegetation also increases during this interval. Included are Artemisia, Cheno-Ams, Cercocarpus-Purshia-type, Ambrosia, Chrysolepis, and Quercus vaccinifolia. The trend in shrub pollen covaries with pollen and macrofossil records in Mono Lake and the Owens Valley.

The Pleistocene to Holocene transition at Tule Lake is indicated by an initial decrease in Juniperus followed by a rise in Pinus pollen at the expense of sagebrush. High fluctuating Cyperaceae (sedge) and Typha (cattail) percentages are also attributed to the lowering of the lake level and expansion of surrounding marshes at two intervals in the Holocene.

Pollen from Owens Lake and the Alabama Hills pack rat middens documents a continuing regional postglacial vegetation change after 10,000 yr B.P. As Juniperus pollen diminishes to low values, Pinus begins to peak with the increase of Abies and such xeric shrub pollen as Cercocarpus-Purshia-type, Ephedra, Ambrosia, and Cheno-Ams. Macrofossils date the local appearances of Krascheninnikovia lanata (winterfat), Chrysothamnus teretifolius (rubber rabbitbrush), Grayia spinosa (spiny hopsage), Lycium andersonii (wolfberry), and Mirabilis bigelovii (four o'clcock) between 9540 yr B.P. and 8700 yr B.P. as additions to the xeric association previously established in the Alabama Hills. Juniperus osteosperma finally departed from the locality between 9500 and 7650 yr B.P.

An early Holocene macrofossil assemblage was taken from two pack rat middens located in Falls Canyon on the northwest slope of the White Mountains (Jennings and Elliott-Fisk 1993) at the lower range of the piñon/mountain mahogany–sagebrush (Artemisia nova)–desert bitterbrush woodland (1,830 m [6,004 ft]). They are radiocarbon-dated to 8790 yr B.P. and 7810 yr B.P. The middens reflect the modern community except for the lack of such xeric shrubs as Cercocarpus ledifolius, Ephedra viridis, and Purshia tridentata var. glandulosa. The oldest midden provides a minimum date for Pinus monophylla in the White Mountains; because there is no glacial-to-Holocene chronological sequence for the mountain front, it cannot be affirmed as the earliest date of occurrence. Dispersal of P. monophylla into the White Mountains, however, may be close to the early Holocene if the populations had retreated to the southern desert mountains as they did in the Great Basin. The 9830 yr B.P. Volcanic Tableland midden did not contain P. monophylla, although that area was suitable habitat during the late-glacial. The northernmost full-glacial occurrences of the species are at equivalent latitudes from 1,155 m (3,790 ft) at the western base of the southern Inyo Mountains (36°36' N) dated between 22,900 yr B.P. and 17,680 yr B.P. (Koehler and Anderson 1994a) and from a 925 m (3,035 ft) site in the Skeleton Hills in the northern Mojave Desert of southwest Nevada (36°38' N) dated to 17,900 yr B.P. (Spaulding et al. 1990). Both sites have a southeast aspect. P. monophylla moved north or upslope as climatic conditions became favorable, presumably when warming summers were accompanied by an expansion of monsoonal rainfall in the Southwest deserts (Spaulding and Graumlich 1986). The species arrived at the southern slopes of the Eleana Range, 50 km (30 mi) north of the Skeleton Hills and 885 m (2,900 ft) higher, by 11,700 yr B.P., so it is not unreasonable to expect it to have dispersed 106 km (66 mi) north and 675 m (2,215 ft) higher along a more continuous mountain range at a faster rate.

Farther south along the mountain front, a 5640 yr B.P. midden from near the head of Silver Canyon (3,048 m [10,000 ft]) contains J. osteosperma and P. monophylla macrofossils. This is evidence for the extension of the upper limits of these trees to elevations now occupied by bristlecone pine–limber pine woodland, presumably as a consequence of higher temperatures.

Middle to Late Holocene (6.0 ka to Present)

West-Slope Sierra Nevada

The general trends in pollen abundances at intermediate elevations over the past 6,000 years are a decrease in oak and alder from their early Holocene maxima and an increase in Abies and Cupressaceae (*Calocedrus decurrens*). Charcoal concentrations also decrease. More effective moisture, from a combination of lower temperatures and higher levels of precipitation, are suggested by these data. Change in climate parallels the postulated lessening of summer insolation over the Northern Hemisphere toward present values (COHMAP Members 1988). The analysis of temperature-sensitive deuterium to hydrogen ratios (δD values) in bristlecone pine tree rings from the White Mountains has produced an 8,000-year chronology indicating optimal temperatures at 6,800 years ago followed by a continuous average cooling (Feng and Epstein 1994). There have been higher-frequency fluctuations in vegetation dynamics that the temporal resolution of the existing pollen stratigraphies either do not capture or that, when recorded, need to be further analyzed, but overall the modern vegetation communities were developed during this period.

There are some differences in details among sites. Lake Moran displays its usual lag effect, with an increase in Quercus pollen to a maximum frequency at about 4500 yr B.P. Quercus also continues to increase at Osgood Swamp until about 2800 yr B.P. High frequencies of Alnus pollen, along with an abundance of Carex lenticular and Ranunculaceae macrofossils at Nichols Meadow, are interpreted as the establishment of the modern meadow (Koehler and Anderson 1994b). At Balsam Meadow, the synchronous rise in percentages of Abies, *Calocedrus decurrens*, and Quercus pollen and decrease of Pinus pollen during the past 3,000 years are explained as a downslope shift of those species that make up the present community (Davis et al. 1985). Finally, the Log Meadow site shows an increase in Sequoiadendron pollen after 4500 yr B.P. from a very few to maximum abundances of the modern forest during the past several hundred years (Anderson 1994).

The high-altitude sites of Starkweather and Tioga Pass Ponds are sensitive to the response of upper montane and subalpine vegetation to Holocene climate change. They both document the variations of the upper altitudinal limits of red fir and mountain hemlock and the lower range of whitebark pine after 6000 yr B.P. At Tioga Pass Pond, Abies pollen increased to a more-or-less stationary level at about 4000 yr B.P., after several fluctuations during the early Holocene. Beginning with a secondary rise at 2000 yr B.P., Abies rapidly reached maximum values 800 years later. It just as rapidly decreased in abundance soon after, indicating an altitudinal depression. Starkweather Pond, 580 m (1,900 ft) lower, records a gentler upward trend in Abies to 3000 yr B.P. A macrofossil identified as A. grandis was recovered in sediments dated at about 2500 yr B.P. Tsuga mertensiana pollen became abundant just before 5000 yr B.P. as populations approached Tioga Pass Pond. The species arrived 500 years later, depositing needles in the pond sediments, and subsequently retreated about 2500 yr B.P. At the same time, there was a steady increase in mountain hemlock pollen at Ten Lakes, located 2,743 m (9,020 ft) above the Tuolumne River in Yosemite National Park (Anderson 1987). Pinus albicaulis needles are relatively common in Tioga Pass Pond by 3500 yr B.P., remaining at high frequencies until 500 yr B.P.

Anderson (1990a) interprets the collective pattern from all three sites as a response to cooler conditions beginning about 3000-2500 yr B.P., depressing the upper altitudinal limits of Tsuga mertensiana and Abies grandis and the lower limits of Pinus albicaulis. There is widespread evidence for a cool-moist episode between 4000 and 2500 yr B.P. in the Southwest, including a high stand at Mono Lake at 3770 cal yr B.P. (Stine 1990), the lowering of the bristlecone pine upper tree line in the White Mountains between 3500 and 2500 yr B.P. (LaMarche 1973), and the existence of a shallow lake in the Silver Lake playa around 3620 yr B.P. (Enzel et al. 1992), to cite only a few examples.

Pollen and macrofossil profiles compiled from close increment sampling are important for analyzing century-scale vegetation changes. The Woski Pond diagram is one such record (Anderson 1987; Anderson and Carpenter 1991) (figure 4.7). Woski Pond is located in Slaughter House Meadow, Yosemite Valley, at 1,212 m (3,975 ft). The bottom of the core is dated to nearly 1500 yr B.P. (A.D. 1300), and samples were taken at about 50- to 150-year intervals. The lower half of the diagram represents a mixed conifer forest dominated by Pinus ponderosa, Abies, *Calocedrus decurrens*, and Quercus (probably Q. kelloggii). At about 650 yr B.P. there was an abrupt shift in pollen trends to decreasing Pinus and Abies and increasing Quercus and shrub pollen, primarily Prunus- and Cercocarpus-type. A very large spike of charcoal accompanying the shift indicates a fire disturbance event.

There are two lines of evidence leading to the conclusion that the disturbance was not natural but resulted from human intervention. First, around A.D. 1300 the climate began to change from a 400-year series of persistent above-average temperatures (the Medieval Warm Period) to a 500-year period with a temperature mean of 0.48°C (0.86°F) below modern levels and a precipitation mean of 6.46 cm (2.64 in) above modern averages in the southern Sierra Nevada, based on tree-ring analysis (Graumlich 1993). These conditions produced a positive glacier budget with multiple advances of alpine glaciers and a decrease in the number of fire events (Birman 1964; Burke and Birkeland 1983; Curry 1969; Gillespie 1982; Scuderi 1984, 1987; Swetnam 1993). This is the worldwide Little Ice Age, also termed the Matthes glaciation in the Sierra Nevada. The change in direction of pollen percentages in Woski Pond runs counter to what would be expected with a cooler, wetter climate phase. The initial disturbance could be explained as the cumulative effect of the previous period of droughts. The high-frequency charcoal influx between 800 and 600 yr B.P. is obvious evidence for a brief interval of intense local fires that altered the forest structure. It does not

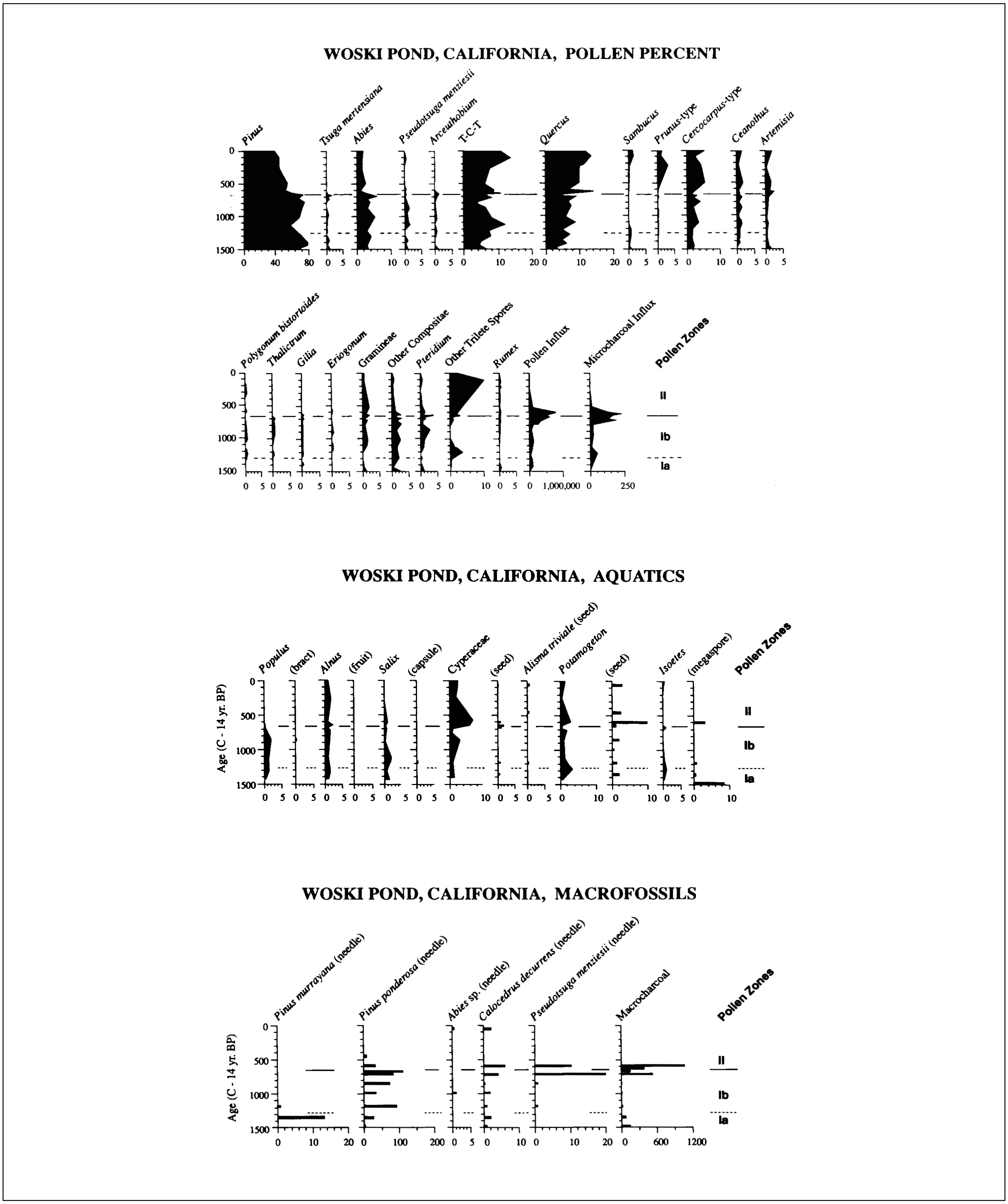


FIGURE 4.7

Pollen and macrofossil profile of Woski Pond, Yosemite National Park (from Anderson and Carpenter 1991).

explain, however, the continued decline in Pinus pollen and increase in Quercus pollen. Second, archaeological investigations document that after A.D. 1200 Yosemite Valley was permanently occupied by a large, sedentary population of Native Americans who exploited a wide variety of resources, particularly the acorn (Munday and Hull 1988). The similarity of their material culture relates this population to the historically known Central Sierra Miwok. The Miwok, like other California groups, practiced intensive vegetation management, including the use of fire (Blackburn and Anderson 1993). Correlation of the dates of human settlement, the large charcoal peak, and rapid, sustained vegetation change supports a strong case that the human inhabitants of Yosemite initially burned the forest for conversion to an open oak woodland in order to enhance the acorn crop, among other reasons. Fire may have been used periodically to maintain the vegetation type. The scope of this report, as a summary of existing studies of vegetation history, encompasses primarily the vegetation-climate relationship, but for future research it is strongly recommended that prehistoric human modification of the landscape be taken into account.

East-Side Sierra Nevada

The situation of Barrett Lake at the present lower elevational limit of Tsuga mertensiana and the upper limit of Abies grandis makes it a sensitive site for recording vegetation change. Arboreal pollen increased around the lake after 5500 yr B.P., when A. grandis was added to the previous lodgepole pine–limber pine–mountain hemlock forest and the T. mertensiana population grew. Pollen abundances peaked around 1000 yr B.P. before declining.

The remaining three middens to be considered from the southern end of the White Mountains, dating from 4510 to 2130 yr B.P., contain macrofossil assemblages that are little different from the modern flora at the sites. Similarly, only small changes are evident from the Alabama Hills midden assemblages. Cowania mexicana disappeared from the record, and Echinocactus polycephalus (cottontop cactus) was added to the flora after 2830 yr B.P.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

A great deal of information about vegetation dynamics in the Sierra Nevada region exists from paleoecological data. The information is at a fairly coarse temporal and spatial scale, however. In order to resolve the scale to a finer level, a finer network of sites in all vegetation communities and at the full range of elevations would be needed. Research is continually providing new sites: the Desert Research Institute (DRI) is analyzing cores retrieved from Eagle Lake and Pine Creek drainage in northern California; Little Valley in the Washoe Lake area; and a series of subalpine ponds and meadows in the Desolation Wilderness, the headwaters of Lee Vining Creek, the Middle Fork of Bishop Creek, and the North Fork Kings River (Wigand 1994). A joint project between DRI and the U.S. Geological Survey is a study of macrofossils from an exposure of glacial and interglacial deposits in the Feather River canyon spanning the past 600,000 years (Wigand 1994).

The study of vegetation history is critical to management. Most important is the realization that the global climate system and climatically sensitive elements of the ecosystem, including vegetation, are in a constant state of flux. The nature and degree of climatic control of ecosystem processes, however, can be usefully conceptualized by specifying the spatial and temporal scales of interest. Change can be slow or very rapid, and the range of variability is much greater than that observed during our lifetimes or even recorded over the past century. In addition, some climatic and ecosystem changes are quasi-periodic and thus somewhat predictable; other changes are chaotic and strongly influenced by historical contingencies, frustrating any definite projections of future outcomes.

The long-term perspective has shown that plant communities we recognize today are not cohesive units but disassemble and reassemble with varying dominance patterns and composition in response to climatic variation; each species responds individualistically at its own rate, some lagging behind others, and never quite in equilibrium. Associations of species have occurred in the past for which no known modern analog can be found, implying that the full range of potential responses of taxa may not be expressed in the modern climate state. This individualistic behavior of vegetation communities (Gleason 1926) does not deny the competitive interactions between species that make any community whole "greater than the sum of its parts." It does mean that, at any one time, the landscape is a unique combination of climate, species, soils, and topography (see also Sprugel 1991).

Because the management concepts of habitat type and potential natural vegetation assume stability and a single pathway toward a specific endpoint of species composition, they need to be modified to account for uncertain changes in environmental conditions and a multiplicity of possible future states (Tausch et al. 1993). Management principles that have the achievement and maintenance of a steady-state vegetation community as an objective may be successfully applied on a small scale with concerted effort. But sustaining an entire landscape or achieving a single desired hypothetical landscape over the long term is not feasible. With insight from paleoecology, the focus of management should be "the maintenance of the dynamic capacity [of an ecosystem] to respond adaptively" (Costanza et al. 1993). This focus requires knowledge of the processes operating at present and in the past and working with those processes to allow a system enough resilience to respond to changing circumstances. The structure and function of an ecosystem may be sustained even though the species composition will vary. Close monitoring and continual adjustment in management practices is still necessary. In any case, more research is needed to acquire knowledge sufficient to understand and predict the future behavior of ecosystems and their response to climate change (Mooney 1991).

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NOTES

1. The following sites record subalpine sagebrush steppe–woodland above 1,500 m (4,900 ft):

   Swamp Lake, Yosemite National Park, 1,554 m (5,098 ft), Tuolumne River drainage, white fir–mixed conifer forest (Smith and Anderson 1992)

   McMurray Lake, 1,778 m (5,832 ft), Yuba River drainage, red fir–mixed conifer forest (Byrne et al. 1993)

   Swamp Lake, 1,957 m (6,420 ft), North Fork Stanislaus River drainage, white fir–mixed conifer forest (Batchelder 1980)

   Burgson Lake, Stanislaus River drainage, 1,960 m (6,430 ft), red fir–mixed conifer forest (Byrne et al. 1993)

   Osgood Swamp, 1,980 m (6,500 ft), Lake Tahoe Basin, mixed conifer (Adam 1967)

   Lily Pad Lake, 1,980 m (6,500 ft), North Fork Kings River drainage, white fir–mixed conifer forest (Byrne et al. 1993)

   Bunker Lake, 1,995 m (6,550 ft), Middle Fork American River drainage, upper margin white fir–mixed conifer forest near red fir forest (Edlund 1994)

   Balsam Meadow, 2,015 m (6,611 ft), San Joaquin River drainage, upper margin white fir–mixed conifer near red fir forest (Davis et al. 1985)

   Lake Moran, 2,018 m (6,621 ft), North Fork Stanislaus River drainage, red fir forest (Edlund 1991; Edlund and Byrne 1991)

   Exchequer Meadow, 2,219 m (7,280 ft), Kings River drainage, Jeffrey pine forest (Davis and Moratto 1988)

   Starkweather Pond, 2,438 m (8,000 ft), Middle Fork San Joaquin River drainage, red fir forest (Anderson 1987, 1990a)

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APPENDIX 4.1

Quaternary Pollen and Macrofossil Sites in the SNEP Study Area

				Elevation		
Site	County	Latitude	Longitude	m	ft	Reference
Tulelake	Siskiyou	41°57'	121°30'	1,229	4,030	Adam et al. 1990; Adam et al. 1989
Eagle Lake	Lassen	40°35'	120°45'	1,500	4,920	Wigand 1994
McMurray Lake	Sierra	39°27'	120°39'	1,778	5,832	Byrne et al. 1993
Ross Relles Camp	Nevada	39°22'	120°57'	900	2,950	West n.d.
Tahoe City	Placer	39°10'	120°09'	1,900	6,175	Adam 1973
Bunker Lake	Placer	39°03'	120°23'	1,995	6,545	Edlund 1994
Osgood Swamp	El Dorado	38°51'	120°02'	1,980	6,500	Adam 1967; Zauderer 1973
Upper Echo Lake	El Dorado	38°50'	120°04'	2,300	7,550	Adam n.d.b
Ralston Ridge Bog	El Dorado	38°50'	120°06'	2,580	8,465	Sercelj and Adam 1975
Auburn Dam	El Dorado	38°50'	120°69'	100	330	Kilbourne 1978
Meyers Grade Marsh	El Dorado	38°50'	120°50'	2,073	6,800	Dorland 1980; Dorland et al. 1980
Grass Lake	El Dorado	38°48'	119°58'	2,347	7,700	Dorland 1980; Dorland et al. 1980
Gabbot Meadow	Tuolumne	38°25'	120°52'	1,995	6,550	Mackey and Sullivan 1991
Lake Moran	Tuolumne	38°23'	120°08'	2,018	6,621	Edlund 1991; Edlund and Byrne 1991
Swamp Lake	Tuolumne	38°22'	120°08'	1,957	6,420	Batchelder 1980
Burgson Lake	Tuolumne	38°21'	119°56'	1,960	6,430	Byrne et al. 1993
Tule Lake	Mono	38°21'	119°28'	2,079	6,820	Byrne et al. 1979
Catfish Lake	Tuolumne	38°12'	119°59'	1,850	6,070	Byrne n.d.
Mono Lake	Mono	38°00'	119°10'	1,950	6,400	Davis 1993
Swamp Lake, YNP	Tuolumne	37°57'	119°49'	1,554	5,100	Smith and Anderson 1992
Ten Lakes #3	Tuolumne	37°54'	119°32'	2,743	9,020	Anderson 1987
Tioga Pass Pond	Mono	37°54'	119°15'	3,018	9,900	Anderson 1987, 1990a
Soda Springs	Mariposa	37°53'	119°22'	2,750	9,022	Adam 1967
Polly Dome	Mariposa	37°51'	119°27'	2,650	8,700	Batch 1977
Black Lake	Mono	37°49'	118°35'	1,900	6,230	Batchelder 1970
Crane Flat	Mariposa	37°46'	119°48'	1,850	6,070	Adam 1967
Woski Pond	Mariposa	37°43'	119°37'	1,212	3,975	Anderson 1987
Hodgdon Ranch	Mariposa	37°41'	119°52'	1,400	4,590	Adam 1967
McGurk Mdw.	Mariposa	37°41'	119°38'	2,091	6,860	Anderson and Smith 1994
Starkweather Pond	Madera	37°40'	119°04'	2,438	8,000	Anderson 1987, 1990a
Barrett Lake	Mono	37°36'	119°00'	2,816	9,240	Anderson 1987, 1990a
Nichols Meadow	Madera	37°26'	119°34'	1,509	4,950	Koehler and Anderson 1994b
White Mountains	Mono	37°20' to 37°45'	118°05' to 118°25'	1,341 to 3,048	4,400 to 10,000	Jennings and Elliott-Fisk 1993
Lake 11,100 ft.	Fresno	37°12'	118°41'	3,380	11,100	Adam n.d.a
Deep Springs Valley	Mono	37°11'	118°03'	1,500	4,920	Woolfenden n.d.
Balsam Meadow	Fresno	37°09'	119°14'	2,015	6,610	Davis et al. 1985
Exchequer Meadow	Fresno	37°04'	119°06'	2,219	7,280	Davis and Moratto 1988
Dinkey Meadow	Fresno	37°00'	119°05'	1,683	5,520	Davis et al. 1985
Lily Pad Lake	Fresno	36°59'	118°59'	1,980	6,500	Byrne et al. 1993
Kings Canyon	Fresno	36°52'	119°17'	920 to 1,270	3,018 to 4,167	Cole 1983
Hightop Meadow	Fresno	36°48'	118°57'	1,908	6,260	Anderson and Smith 1994
Meadow of Honor	Fresno	36°44'	118°59'	1,857	6,090	Anderson and Smith 1994
Weston Meadow	Tulare	36°43'	118°53'	2,036	6,680	Anderson and Smith 1994
Owens Lake	Inyo	36°36'	118°05'	1,155	3,790	Koehler and Anderson 1994a
Long Meadow	Tulare	36°35'	118°44'	2,206	7,240	Anderson and Smith 1994
Circle Meadow	Tulare	36°34'	118°45'	2,085	6,840	Anderson and Smith 1994
Log Meadow	Tulare	36°33'	118°44'	2,048	6,720	Anderson 1994
Alabama Hills	Inyo	36°32' to 36°37'	118°03' to 118°07'	1,264 to 1,535	4,150 to 5,040	Koehler and Anderson 1995
Alabama Hills	Inyo	36°22'	118°07'	1,400	4,600	Axelrod and Ting 1962
Owens Lake	Inyo	36°22'	117°58'	1,100	3,600	Litwin et al. 1995
Ramshaw Meadows	Inyo	36°13'	118°13'	2,620	8,600	Axelrod and Ting 1962
Dogwood Meadow	Tulare	36°12'	118°40'	1,987	6,520	Anderson and Smith 1994
Bakeoven Meadows	Inyo	36°08'	118°10'	2,440	8,000	Axelrod and Ting 1962
Kennedy Meadows	Inyo	36°00'	118°14'	1,890	6,200	Axelrod and Ting 1962
Little Lake	Inyo	35°57'	117°54'	1,000	3,280	Mehringer and Sheppard 1978
Little Lake	Inyo	35°56'	117°53'	1,020	3,360	Axelrod and Ting 1962
Robber's Roost	Kern	35°35'	117°57'	1,215	4,000	McCarten and Van Devender 1988

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